

THE EFFECTS OF POPULATION DENSITY AND FOOD
QUALITY ON REPRODUCTIVE OUTPUT IN THE FEMALE
GUPPY, POECILIA RETICULATA (PETERS)

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Title and subtitle The effects of population density and food quality on reproductive output in the female guppy, <i>Poecilia reticulata</i> (Peters).		
Abstract Laboratory experiments, microscopy and dissections were performed with female guppies, <i>Poecilia reticulata</i> (Peters) to investigate: (1) Influences of population density on individual fecundity and fertility under conditions of ad libitum regimens and food restriction. (2) Effects of protein, carbohydrates and lipids on reproductive success. <u>Population density, food restriction, reproduction:</u> Fecundity was significantly higher in low densities of 16 females compared with populations of 31 individuals living in ordinary or conditioned aquarium water. A significantly increased fecundity existed among females of one and two gestation periods from low densities of 10 individuals compared with groups of either 20 or 40 females. Fertility was significantly improved in females of one and two gestation periods when exposed to densities of 10 individuals compared with densities of 40 females. A significantly reinforced number of ova plus vitellogenic oocytes per female (reproductive output) existed in densities of 16 females compared to densities of 31 individuals. Embryo size and ovum diameter were significantly larger at high densities (40 females) than at low densities (10 individuals). Females of one pregnancy from densities of 10 individuals exhibited significantly greater ovarian length, width, height, volume and weight compared with groups of 30 females. Gonad dimensions and weight were significantly larger among females with two gestation periods in low densities of 10 individuals than in populations of 20 females. Significantly higher ovarian width, height and volume existed in densities of either 12, 16 or 20 females compared with populations of 30 individuals. Average gonadosomatic index increased with reduced population densities. <u>Population density, ad libitum regimens, reproduction:</u> Insignificant differences of the examined variables existed between different densities when given excess food amounts. <u>Food quality, reproduction:</u> Significantly improved fecundity and reproductive output prevailed among females ingesting 72 % protein than in groups exploiting either 53, (cont.) Key words <i>Poecilia reticulata</i>, Protein, Carbohydrates, Lipids, Fecundity, Fertility, Intrafollicular gestation, Embryos, Zygotes, Ova, Vitellogenic oocytes, Pre-vitellogenic oocytes.		
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TORSTEN DAHLGREN
FIL. KAND., LD

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LUND 1981

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IN HISTORICAL PERSPECTIVE

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TORSTEN DANLÖF

DEPARTMENT OF ANIMAL ECOLOGY
UNIVERSITY OF LUND, SWEDEN



LUND 1981

The present doctoral dissertation is a summary of the following papers and manuscripts referred to by Roman numerals in parentheses:

- (I) Dahlgren, B.T. (1979). The effects of population density on fecundity and fertility in the guppy, *Poecilia reticulata* (Peters). J. Fish Biol. 15, 71-91.
- (II) Dahlgren, B.T. (1980). The effects of three different dietary protein levels on the fecundity in the guppy, *Poecilia reticulata* (Peters). J. Fish Biol. 16, 83-97.
- (III) Dahlgren, B.T. (1980). The influence of three dietary non-protein levels on fecundity and fertility in the guppy *Poecilia reticulata*. Oikos 34, 337-346.
- (IV) Dahlgren, B.T. (1980). Influences of population density on reproductive output at food excess in the guppy, *Poecilia reticulata* (Peters). Biol. Reprod. 22, 1047-1061.
- (V) Dahlgren, B.T. Relationships between population density and reproductive success in the female guppy *Poecilia reticulata*. Under editorial consideration.
- (VI) Dahlgren, B.T. The impact of different dietary protein contents on fecundity and fertility in the female guppy, *Poecilia reticulata* (Peters). Under editorial consideration.
- (VII) Dahlgren, B.T. Effects of carbohydrates and lipids on reproductive output in the female guppy, *Poecilia reticulata* (Peters). Under editorial consideration.

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I. INTRODUCTION

I.1. Investigations:

The aim of the present laboratory experiments on guppy females, *Poecilia reticulata* (Peters) was to investigate: (a) The effects of population density on individual fecundity and fertility under conditions of food restriction and food excess. (b) Influences of protein, carbohydrates and lipids on individual reproductive success.

I.2. Reproductive cycle:

The male intromittent organ, gonopodium (Goodrich et al., 1934) makes transfer of spermatophores to the oviduct possible. Spermatozoa disintegrate and reach a dorsal evagination of the unpaired ovary (Kadow, 1954). Sperm storage in ovarian tissues may last for 8 months (Whitney & Hahnel, 1964) and the duration between copulation and intrafollicular fertilization takes at least 24 hours (Rosenthal, 1952). Internal fertilization is accompanied by an intrafollicular gestation. Viviparity (Rosenthal, 1951) or ovoviviparity (Fontaine, 1945) exist. The gestation period, progressing from fertilization to parturition, extends from 21 to more than 30 days (Dépêche & Schoffeniels, 1975; Rosenthal, 1952; Scrimshaw, 1944). Gestation is followed by parturition and a quiescent state of 5 or 9 - 12 days implying vitellogenesis and a new pregnancy (Dildine, 1936; Rosenthal, 1952).

I.3. Pertinent record:

The literature offers very restricted information on effects of population density and food quality on reproductive success in fish.

I.4. Population studies (I,IV,V):

Fertility investigations on the guppy, *Poecilia reticulata* have indicated that potential capacity to produce living progeny was inversely correlated with population density when examined after parturition (Rose, 1959; Warren, 1973 a, b, c). Experiments on fecundity in carp, *Cyprinus carpio* pointed to a reduced ability for development of ova under conditions of high densities (Yoshihara, 1952) and depression of oviposition rates was the effect of prevailed crowding in medaka, *Oryzias latipes* (Kawaziri, 1950). A pronounced rate of egg retention was induced in pink salmon, *Oncorhynchus gorbuscha* by the existence of a high population density in chum salmon, *Oncorhynchus keta* (Semko, 1954). Periods of increased densities in the guppy, *Poecilia reticulata* caused an intensified rate of aggression (Farr & Herrnkind, 1974), whereas reproductive features such as gonopodial swings and sigmoid displays were suppressed (Warren, 1973 c). Inverse correlations between growth and population density have been demonstrated in channel catfish, *Ictalurus punctatus* (Walker & Carlander, 1970), brown trout, *Salmo trutta* (Le Cren, 1962) and sockeye salmon, *Oncorhynchus nerka* (Krogus, 1961). Specific water-borne products or excretions have been found to act as phe-

romones during high densities as repressive factors inhibiting reproductive cycles and growth. This was indicated in brown trout, *Salmo trutta* (Brown, 1946), guppy, *Poecilia reticulata* (Rose, 1959), goldfish, *Carassius auratus*, carp, *Cyprinus carpio* and *Megastomatobus cyprinella* (Swingle, 1953). Social facilitation (Crawford, 1939) of the feeding behaviour refers to increment in frequency and intensity of food consumption in presence of other individuals. This phenomenon is of great importance in the context of population studies (IV) and has been demonstrated in different fish species, i.a. the guppy, *Poecilia reticulata* (Uematsu, 1971 a, b), green sunfish, *Lepomis cyanellus* (Greenberg, 1947), emerald shiner, *Notropis atherinoides* and paradise fish, *Macropodus opercularis* (Welty, 1934).

I.5. Nutritional studies (II,III,VI,VII):

Fertility was decreased by depression of food supply in the guppy, *Poecilia reticulata* (Hester, 1964) and mosquito fish, *Gambusia affinis* (Krumholz, 1948). Improved food amounts were found to induce an increased weight gain in fathead minnow, *Pimephales promelas* (Smith et al., 1978), three-spined stickleback, *Gasterosteus aculeatus* (Wotton, 1973) and guppy, *Poecilia reticulata* (Davis, 1968). A higher growth rate was caused by ameliorated food rations in brown trout, *Salmo trutta* (Elliott, 1975), perch, *Perca fluviatilis* (Le Cren, 1958) and guppy, *Poecilia reticulata* (Silliman, 1968). The effects of protein on body weight and food conversion were studied in channel catfish, *Ictalurus punctatus* (Dupree, 1967) and improvement of food quantity caused an earlier sexual maturity in brown trout, *Salmo trutta* (Bagenal, 1969; McFadden et al., 1965) and an increased fecundity in roach, *Rutilus rutilus* (Lyagina, 1975) and three-spined stickleback, *Gasterosteus aculeatus* (Wotton, 1973). Food shortage may have been responsible for suspension of vitellogenesis, resorption of oocytes and a decreased fecundity in the goldfish, *Carassius auratus* (Bekker, 1958). Food restriction reduced fecundity through follicular atresia in rainbow trout, *Salmo gairdneri* (Scott, 1962), whereas protein-rich diet significantly influenced spawning in carp, *Cyprinus carpio* (Bieniarz et al., 1977). Increment of the dietary protein level induced a higher growth rate in channel catfish, *Ictalurus punctatus* (Tie-meier et al., 1965) and influences of carbohydrates on weight gain and food conversion were demonstrated in the same species (Dupree & Sneed, 1966).

II. MATERIALS AND METHODS

Details are presented in papers and manuscripts (I - VII).

(1) Silicone glued glass aquaria (56 and 32 l) were used and provided with thermostats, gravel (2 - 3 mm), aeration, circulation and filtration systems.

(2) pH and oxygen saturation were controlled by electrometric methods. Total hardness and carbonate hardness (dH) were examined titrimetrically.

(3) *Aponogeton*, *Echinodorus* and *Cabomba* were planted in equal number per aquarium.

(4) Light (40 W) was on during 12 h (Gorlick, 1976; Liley, 1968; Silliman, 1968; Silliman & Gutsell, 1958) or 14 h per day.

(5) Carefully evaluated feeding schedules were adopted for each experiment. Ground commercial dry food of protein, carbohydrates and lipids was administered (± 0.1 mg) and dry Tubifex was offered under conditions of ad libitum regimens.

(6) Guppies, *Poecilia reticulata* were used and homogeneous populations of virgin females and adult males (King Cobra, Tuxedo Bronze) were randomly distributed to the aquaria.

(7) Experimental procedure: After initial stages males were removed to ensure a synchronized time-table for copulation and fertilization between different populations (Rosenthal, 1952). Intrafollicular gestation periods of 21 - 30 days (Dépêche & Schoffeniels, 1975; Rosenthal, 1952; Scrimshaw, 1944; Stolk, 1951) were adopted and sometimes prolonged. Females were killed at the estimated time for parturition with Tricaine methanesulphonate. Fixation in toto was accomplished in 4 % formalin.

(8) Total body size, standard length (modified standard length) and total body weight (Lagler et al., 1962) were recorded for each female (Definitions: I - VII).

(9) Dissections: A binocular stereoscopic microscope (X8-X30) was used. After gonadal excision, the oviduct and mesovarium were removed. Ovarian length, width, height (± 0.1 mm) and gonad weight (± 0.1 mg) were determined. Direct counting and measurements (± 0.1 mm) were achieved for each female concerning all embryos (Dildine, 1936; Tuge, 1938), zygotes (2.0 - 2.1 mm. Scrimshaw, 1946), ova (0.7 - 2.1 mm. Rosenthal, 1952; Scrimshaw, 1946) and vitellogenic oocytes (0.1 - less than 0.7 mm).

(10) Embryos and ova were preserved in 4 % formalin for total lipid analyses using the methanol-chloroform (1:2) extraction method. Phospholipids, free fatty acids, triglycerides and sterols were analysed by thin-layer chromatography.

(11) Females were classified as adults when their body length was 20.0 - 25.4 mm (Chacko, 1948; Yamagishi, 1976). Vitellogenic adult females (Dépêche & Schoffeniels, 1975) were identified by intrafollicular ova and vitellogenic oocytes. Pregnant females were recognized by the convex abdomen, embryos and pregnancy spots (Stolk, 1958).

(12) Statistical methods: t-test for independent means, two-variable linear regression analysis and Chi square statistics for 2 x 2 tables with and without Yates' correction. All probability values refer to two-tailed tests.

III. RESULTS AND CONCLUSIONS

III.1. Introductory remarks:

III.1.1.

Roman numerals in parentheses refer to the papers and manuscripts of the dissertation. (A) = Population experiments, (B) = Protein investigations, (C) = Studies of carbohydrates and lipids.

III.1.2.

Nutritional studies dealing with different dietary non-protein amounts (i.e. carbohydrates and lipids) always imply identical protein levels between groups. A special feeding schedule was used in each experiment and all diets contained protein, carbohydrates and lipids. Details concerning amounts and quality of food offered per female are given in I - VII.

III.1.3.

Results from population studies refer to experiments under conditions of food restriction, i.e. limited food amounts and qualitative nutritional supply given per female, except in cases when ad libitum feeding schedules (food excess) are mentioned.

III.1.4.

Conditioned water stands for aquarium water where guppy females had lived (V).

III.1.5.

Correlation coefficients = r and Significance levels = P in the figures.

III.2. Growth:

(A) Total body size, modified standard length and total body weight were significantly improved among females from high population densities with 40 individuals compared with low densities of 10 females (I. $p < 0.01$, $p < 0.001$). This result indicates that true growth rate (neoformation) and total weight gain, including lipid deposition, were pronouncedly reinforced among females exposed to an increased population density. Improved allocations of energy and resources to somatic tissues rather than to the ovary may have occurred in these females.

(B) Significantly higher total body weight and growth were revealed in females ingesting 72 % protein compared with females given either 42 or 23 % dietary protein (VI. $p < 0.001$). Total weight gain was also significantly increased among females fed on either 72, 53, 47 or 31 % protein compared with females given a 15 % protein diet (II, VI. $p < 0.01$, $p < 0.001$). According to these data a noticeably improved growth and body weight were induced among females ingesting a comparatively ameliorated protein-rich diet.

(C) Females consuming an 85 % non-protein diet exhibited a significantly higher total body size, standard length and weight gain than groups living on either 78 or 61 % non-protein material (VII. $p < 0.05$, $p < 0.01$, $p < 0.001$). These three variables were also pronouncedly increased among females fed on a 77 % non-protein food compared with females given only 33 % dietary non-protein (VII. $p < 0.001$). Thus, noticeably improved growth rate and reinforced total body weight occurred in females given a comparatively higher dietary non-protein amount (III, VII).

III.3. Ovarian dimensions and gonad weight:

(A) Significantly higher ovarian length, width, height and volume were demonstrated among females at low densities (10 individuals) compared with populations of 40 females (I. $p < 0.05$,

$p < 0.01$). Ovarian width, height and volume in addition to gonad weight were also appreciably higher in females at densities of either 12 or 20 individuals than in populations of 32 females (V. $p < 0.01$, $p < 0.001$). The present findings elucidate significantly improved ovarian proportions and gonad weights (index of reproductive capacity, McFadden et al., 1965) in females exposed to a comparatively lower population density (I,V). Further, these data suggest that females from the lowest population levels exhibit a higher ability to mobilize nutrients for reproductive purposes and a more pronounced energy allocation to ovarian structures than females from higher densities.

(B) Females consuming either 72 or 53 % protein showed ameliorated ovarian dimensions and gonad weights compared with groups given only 15 % dietary protein (VI. $p < 0.05$, $p < 0.01$, $p < 0.001$). Populations of females fed on a 23 % protein food demonstrated a decrease in gonad size and ovarian weight when compared with females ingesting either 72 or 42 % protein (VI. $p < 0.05$, $p < 0.001$). These results reveal pronouncedly higher gonad proportions and weight gains of the ovary in females exposed to improved protein levels.

(C) Significantly ameliorated values of ovarian length, width, volume and gonad weight were found in females consuming 85 % non-protein compared with females fed on a 61 % non-protein diet (VII. $p < 0.05$). Gonad dimensions and ovarian weight were also significantly increased in groups living on 85 % non-protein material compared with females given 53 % non-protein (III. $p < 0.05$). These findings point to increased proportions and weights of the ovarian tissue in females exposed to diets of high non-protein content (III,VII).

III.4. Relationships between variables:

(A) Significant relationships were revealed whenever ovarian weight was correlated with total body weight and gonad volume (I. Fig. 1) in population densities of either 10, 11, 20, 22, 40 or 44 females (I,IV. $p < 0.01$, $p < 0.001$). This was demonstrated both under conditions of food restriction and food excess. Correlations between gonad volume and total body weight are given in Figs 2 and 3 (I,IV).

(B) Ovarian volume and gonad weight were positively correlated with total body weight in groups fed on either 72, 47, 42, 31, 23 or 15 % protein. A significant association between gonad weight and ovarian volume was also elucidated in these groups (II,VI. $p < 0.05$, $p < 0.01$, $p < 0.001$).

(C) Ovarian volume was highly correlated to gonad weight in different groups living on either 85, 78, 69, 53 or 33 % non-protein material (III,VII. $p < 0.001$). Direct relationships persisted between these two variables when plotted against total body size and total body weight (Fig. 4) in females ingesting diets of either 85, 69 or 53 % non-protein (III. $p < 0.05$, $p < 0.01$, $p < 0.001$).

III.5. Gonadosomatic index:

(A) The average gonadosomatic ratio, representing a fecundity index and calculated from ovarian weight as a percentage of total body weight, increased with a reduced population density (I,V).

(B) A trend towards higher mean gonadosomatic index was indicated in females fed on increased protein amounts (II,VI).

(C) Increased gonadosomatic indices were also found in females ingesting comparatively higher amounts of non-protein material (III,VII).

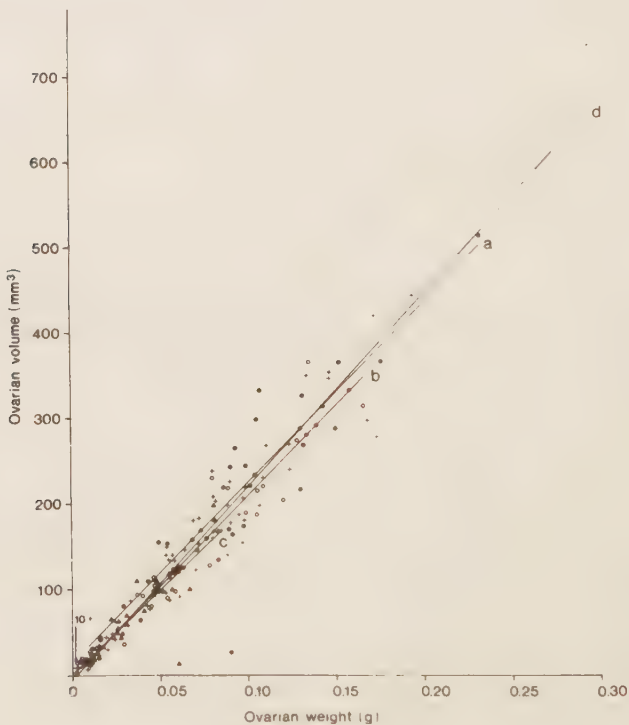


Fig. 1. Correlation between ovarian volume (mm^3) and ovarian weight (g) under conditions of food restriction. ● a = lowest population density (10 females). 1 and 2 gestation periods. $r = 0.9479$, $P < 0.001$. ○ b = Second lowest population density (20 females). 1 and 2 gestation periods. $r = 0.9670$, $P < 0.001$. ▲ c = Population density of 30 females. 1 gestation period. $r = 0.8794$, $P < 0.001$. + d = Highest population density (40 females). 1 and 2 gestation periods. $r = 0.9749$, $P < 0.001$.

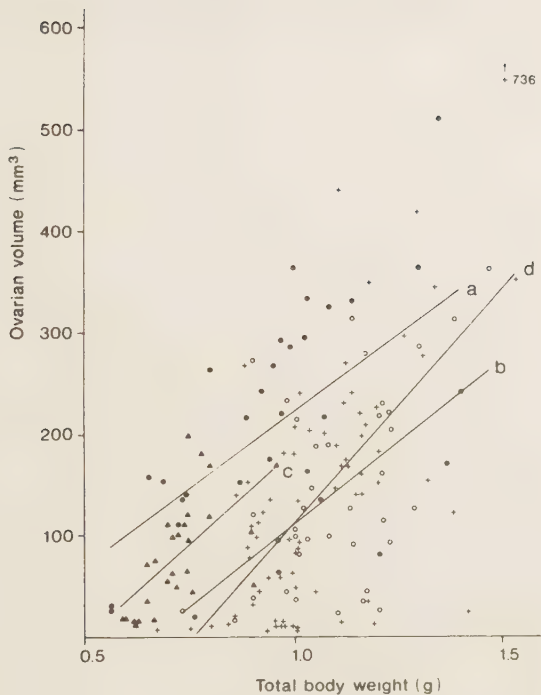


Fig. 2. Relationship between ovarian volume (mm^3) and total body weight (g) under conditions of food restriction. $\bullet$ a = Lowest population density (10 females). 1 and 2 gestation periods. $r = 0.5906$, $P < 0.001$. $\circ$ b = Second lowest population density (20 females). 1 and 2 gestation periods. $r = 0.5146$, $P < 0.001$. $\blacktriangle$ c = Population density of 30 females. 1 gestation period. $r = 0.6225$, $P < 0.001$. $+$ d = Highest population density (40 females). 1 and 2 gestation periods. $r = 0.6008$, $P < 0.001$.

III.6. Reproductive success:

III.6.1. Introductory remarks.

(A,B,C) Fecundity implies (1) absolute reproductive success representing the number of intrafollicular ova per female prior to spawning (Bagenal, 1973) and (2) number of eggs actually

produced by a female (McFadden et al., 1965). Fertility means the number of intrafollicular embryos per individual female. Both fecundity and fertility refer to reproductive success of one female, and in the present dissertation after one and two gestation periods (experimental periods, I - VII).

(1) Population experiments and nutritional studies elucidated an interindividual variation of fecundity and fertility inde-

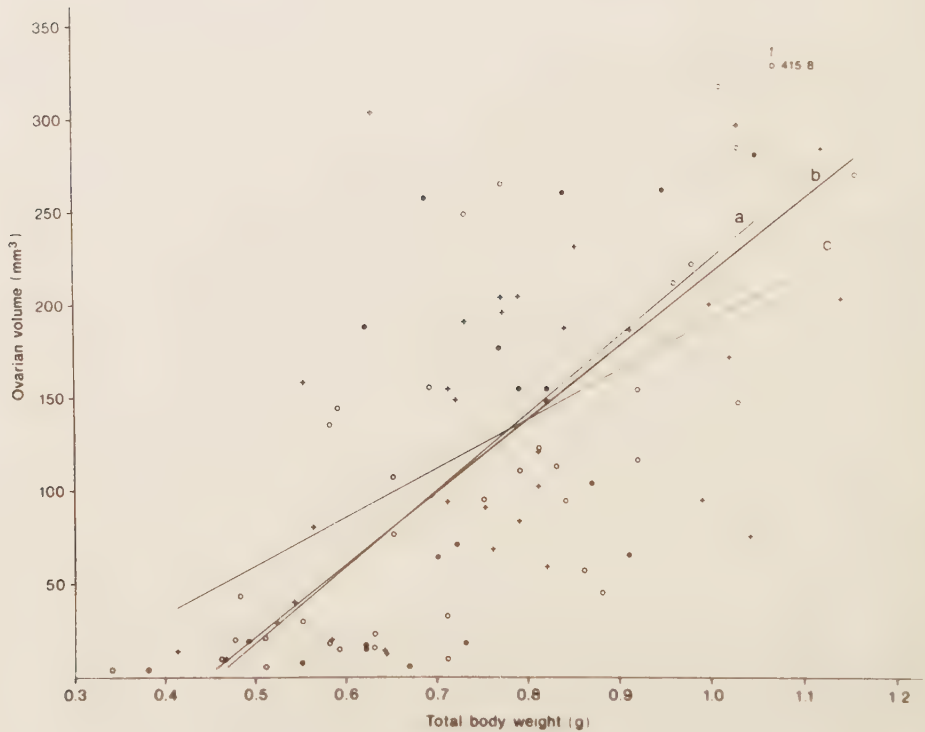


Fig. 3. The relationship between ovarian volume (mm^3) and total body weight (g) when feeding ad libitum. ● a = Lowest population density (11 females). $r = 0.6621$, $P < 0.01$. ○ b = Second lowest population density (22 females). $r = 0.7453$, $P < 0.001$. + c = Highest population density (44 females). $r = 0.5712$, $P < 0.001$.

pendent of population density and food type (I - VII). (2) Females exhibiting different size classes of ova in the ovarian follicles at the same time were also found in all groups of population studies and nutritional experiments (I - VII). (3) Females possessing embryos and ova simultaneously in the gonad were revealed under conditions of different densities and different regimens of protein, carbohydrates and lipids (I - VII).

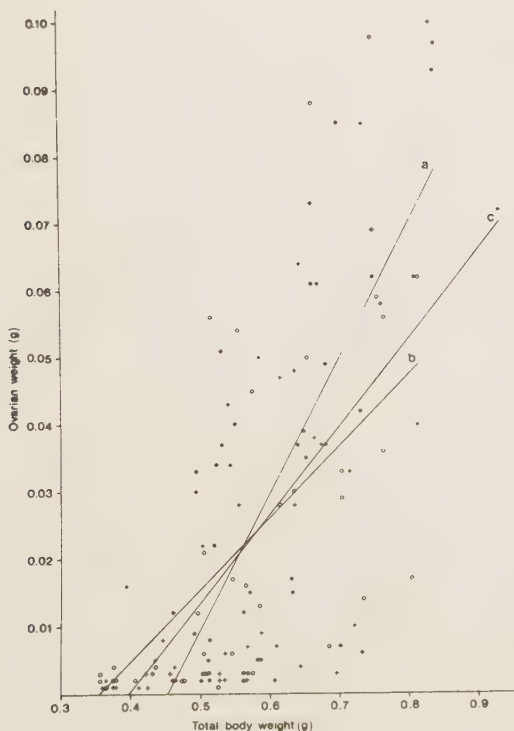


Fig. 4. Ovarian weight (g) plotted against total body weight (g). ● a = Females offered 85 % non-protein. $r = 0.7423$, $P < 0.001$. ○ b = Females offered 69 % non-protein. $r = 0.6368$, $P < 0.001$. + c = Females offered 53 % non-protein. $r = 0.6930$, $P < 0.001$.

This reproductive feature was interpreted as superfoetation (Scrimshaw, 1944; Turner, 1937, 1940).

III.6.2. Fecundity, fertility and further data of population studies.

(A) Individual fecundity was significantly higher in females with one and two gestation periods from low densities of 10 individuals compared with higher densities of either 20 or 40 females (I. $p < 0.01$, $p < 0.001$). Concomitant with this result there also existed a pronounced decrement of ovum diameter at densities of 10 individuals when compared with populations of either 20 or 40 females (I. $p < 0.01$, $p < 0.001$). However, females from most population levels exhibiting a significantly increased fecundity showed no significant reduction of ovum diameter when compared with females at higher densities ($p > 0.05$). These findings point to a pronouncedly high reproductive capacity both concerning number of mature eggs and gamete size among females exposed to low densities (I,V). Individual number of ova was significantly increased at population levels of 16 females compared with densities of 31 individuals living in ordinary or conditioned water (V. $p < 0.01$, $p < 0.001$). Reproductive output, calculated from number of ova and vitellogenic oocytes per female, was also appreciably increased at low densities of 16 individuals compared with populations of 31 females (V. $p < 0.01$). Fertility was found to be significantly reinforced among females of one and two gestation periods from low densities of 10 individuals compared with females at population levels of 40 individuals (I. $p < 0.05$). There also existed a significant decrease of embryo size at low densities of 10 females compared with groups of 40 individuals (I. $p < 0.05$).

III.6.3. Special notes of population studies.

(A) Comparisons between densities of 31 females given ordinary water and females at the same population level exposed to conditioned water revealed no significant differences concerning growth, ovarian dimensions and gonad weight. This was also true for frequency estimations of females in different ontogenetic stages, fecundity and ovum diameter (V. $p > 0.05$).

No significant differences existed between different population densities under conditions of ad libitum feeding schedules in respect to all these variables, fertility and embryo size (IV. $p > 0.05$). The pronounced differences between (1) results from population experiments with food restriction and (2) current findings from population studies of food excess are discussed.

III.6.4. Fecundity, fertility and further data of nutritional studies.

(B) Fecundity was significantly increased among females consuming 72 % protein compared with groups exposed to either a 53, 42 or 23 % protein diet (VI. $p < 0.05$). Likewise, females fed on either 72, 53 or 31 % protein material exhibited an appreciably higher number of ova than groups given food of only 15 % protein (II,VI. $p < 0.05$, $p < 0.001$). These findings point to a vitellogenesis without restraint and higher individual numbers of mature eggs in females living on a high dietary

protein supply. Reproductive output, calculated from number of ova and vitellogenic oocytes per female, was significantly improved in females ingesting 72 % protein compared with populations fed on either 53, 23 or 15 % protein (VI. $p < 0.05$, $p < 0.001$). Increased ovum diameter and size of vitellogenic oocytes were demonstrated in females consuming 72 % protein compared with females fed on a 15 % protein diet (VI. $p < 0.01$, $p < 0.001$). Thus, a significantly larger gamete size and diameter of precursors to ova were found despite the simultaneous increase of individual fecundity among females given 72 % protein. Fertility, embryo size and number of vitellogenic oocytes were only insignificantly influenced by increases and reductions of the dietary protein supply (VI. $p > 0.05$).

(C) Individual fecundity was significantly improved among females exposed to an 85 % non-protein diet compared with populations fed on 61 % non-protein (VII. $p < 0.05$). However, number of vitellogenic oocytes per female was noticeably higher in groups given either 78 or 61 % non-protein than in females fed on an 85 % non-protein diet (VII. $p < 0.001$). This could be the result of a postponed vitellogenesis in females ingesting low non-protein amounts. The diameter of vitellogenic oocytes was smaller in females living on either 78 or 61 % non-protein compared with females consuming 85 % non-protein (VII. $p < 0.001$). Reproductive output, estimated from individual number of ova and vitellogenic oocytes, was significantly higher in females ingesting 78 % non-protein than in groups given 61 % dietary non-protein (VII. $p < 0.01$). Fertility, embryo size and ovum diameter were only insignificantly different between groups fed on different non-protein diets (III, VII. $p > 0.05$).

(A,B,C) Maximum body lengths of large embryos in the present studies were 6.1 - 8.8 mm (V - VII). Values between 6 and 10 mm were demonstrated in earlier works on the guppy (Blaxter, 1969; Chacko, 1948; Dépêche & Schoffeniels, 1975; Dildine, 1936; Goodrich et al., 1934).

III.6.5. Correlations between variables.

(A) Fecundity was positively correlated to ovarian weight at densities of 16 females and also in groups of 31 females exposed to conditioned water and ordinary water (V. Fig. 5. $p < 0.001$). A significant and inverse relationship between number of ova and ovum diameter was found only among females from the two highest densities including 40 and 44 individuals (I, IV. $p < 0.01$, $p < 0.001$).

(B) Number of ova per female plotted against ovum diameter and total body length are given in Figs 6 and 7 (VI).

(C) Fig. 8 demonstrates the relationship between fecundity and total body weight (VII).

III.6.6. Lipids of embryos and ova.

(A,B,C) Lipid analyses indicate that total fat content (dry weight) was comparatively higher in embryos than in ova among females exposed to population densities of either 10, 20, 30 or 40 individuals under conditions of food restriction (I, V) and densities of either 11, 22 or 44 females when food excess was offered (IV). The same findings apply to females ingesting

either 85, 69 or 53 % non-protein material (III). The percentage dry weight of phospholipids (20 - 30 %) and non-polar lipids (i.e. free fatty acids, triglycerides and sterols: 70 - 80 %), estimated from total lipid contents of embryos and ova, was approximately the same at all population densities (V) and all groups of protein studies (VI). Lipid analyses suggest a higher relative amount of free fatty acids in embryos compared with ova and likewise a higher content of phospholipids in ova than in embryos. Phospholipids were mainly represented by lecithin (V,VI).

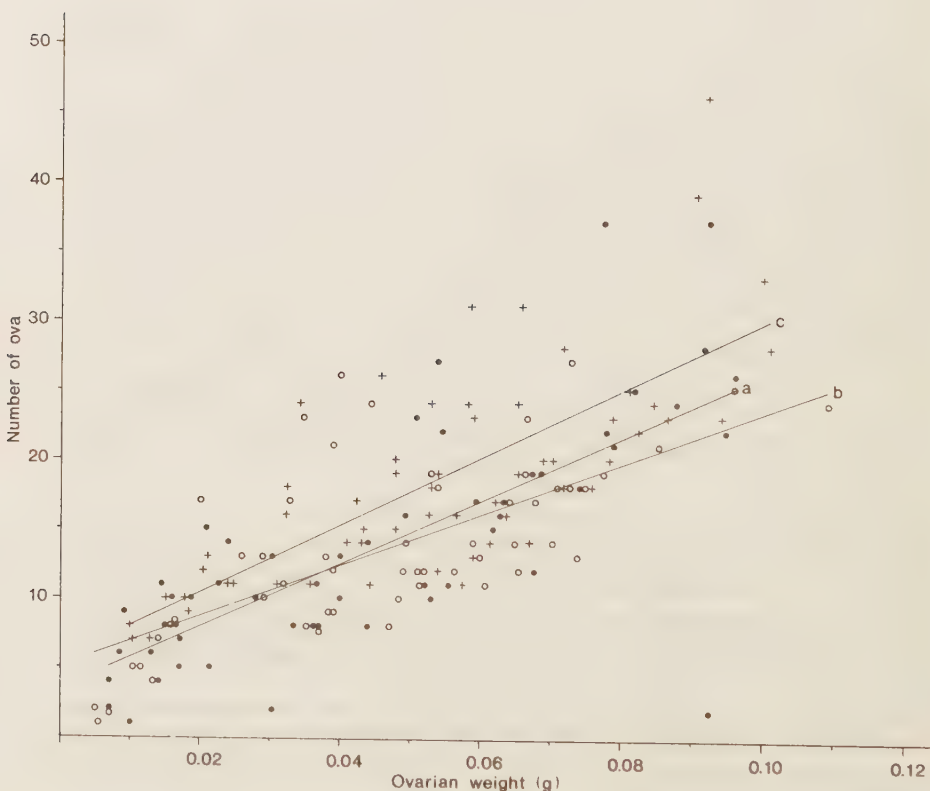


Fig. 5. Correlation between number of ova per female and ovarian weight (g) under conditions of food restriction. ● a = High population density (31 females). $r = 0.7458$, $P < 0.001$. ○ b = High population density (31 females) with conditioned water. $r = 0.6928$, $P < 0.001$. + c = Low population density (16 females). $r = 0.7424$, $P < 0.001$.

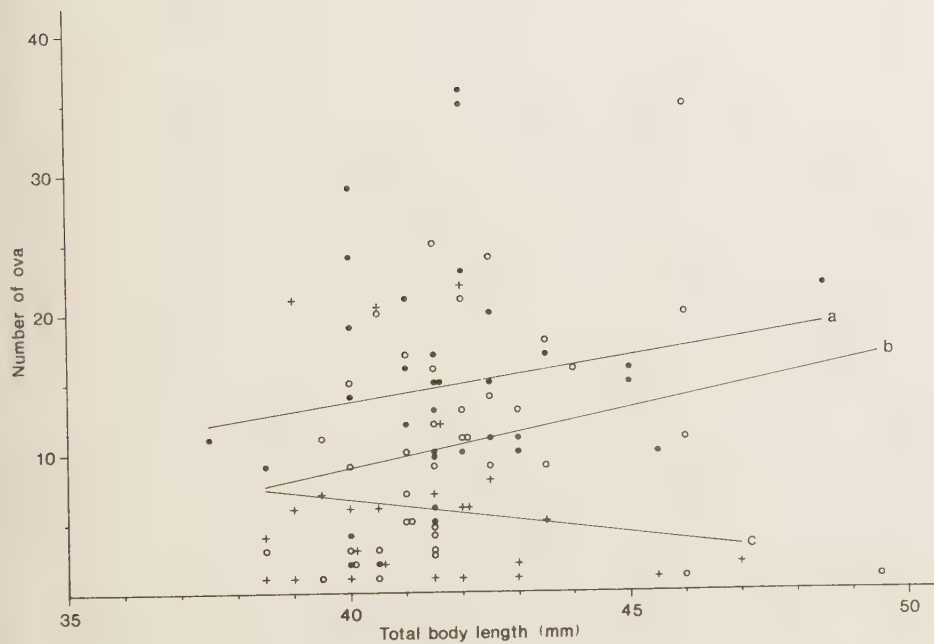


Fig. 6. Number of ova per female plotted against total body length (mm).
 ● a = Females fed on 72 % protein. $r = 0.1633$, $P > 0.05$. ○ b = Females fed on 53 % protein. $r = 0.2374$, $P > 0.05$. + c = Females fed on 15 % protein. $r = -0.1682$, $P > 0.05$.

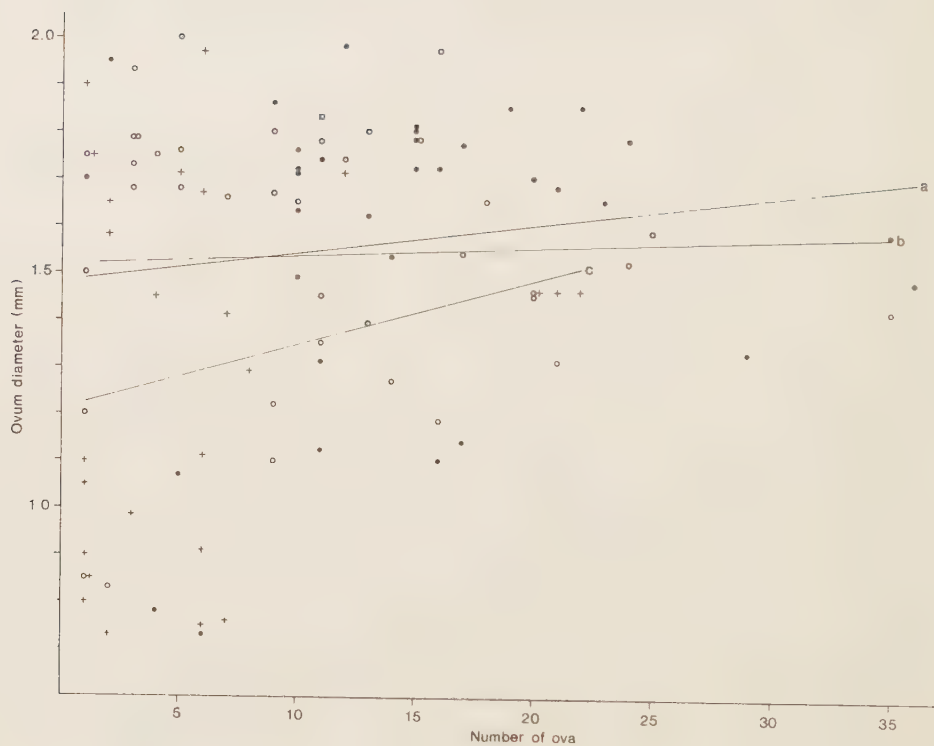


Fig. 7. Relationship between ovum diameter (mm) and number of ova per female.
 ● a = Females given 72 % protein. $r = 0.1448$, $P > 0.05$. ○ b = Females given 53 % protein. $r = 0.0458$, $P > 0.05$. + c = Females given 15 % protein. $r = 0.2175$, $P > 0.05$.

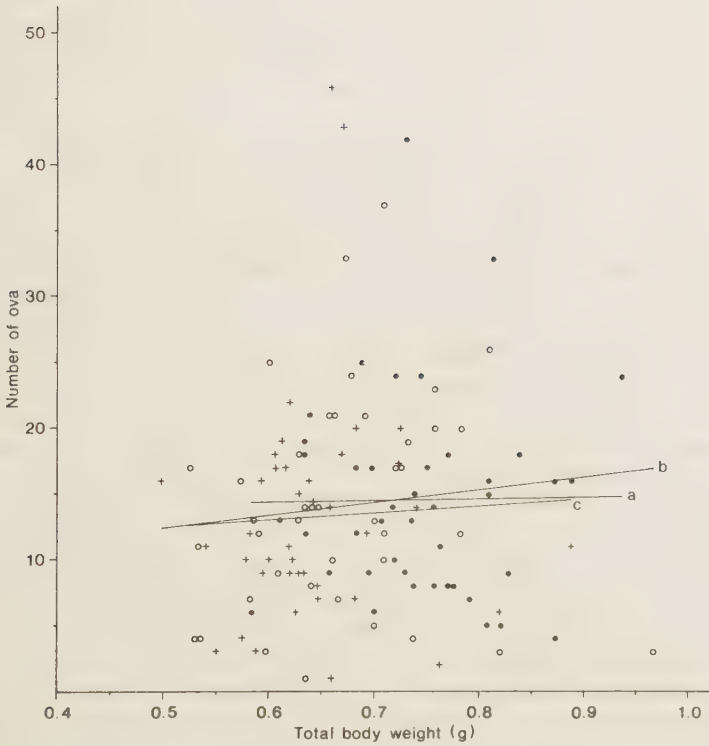


Fig. 8. The correlation between individual number of ova and total body weight (g). ● a = Females ingesting 77 % non-protein. $r = 0.0180$, $P > 0.05$. ○ b = Females ingesting 58 % non-protein. $r = 0.1089$, $P > 0.05$. + c = Females ingesting 33 % non-protein. $r = 0.0455$, $P > 0.05$.

IV. DISCUSSION

IV.1. Population studies (I,IV,V):

The investigations show that an increased population density of guppy females results in a significantly depressed individual fecundity and fertility under conditions of food restriction (I,V). However, this was not the case when ad libitum regimens (food excess) were offered (IV). The present results also indicate that population density has to reach a threshold value in order to induce a significant reduction in fecundity and fertility under periods of food restriction. Decreased reproductive output caused by high population densities indicates the presence of inverse density-dependent mechanisms. Exposition to comparatively low population densities may cause an improved fecundity and fertility to act as a negative feed-back mechanism. Accidental superfoetation (I - VII. Scrimshaw, 1944; Turner, 1937, 1940) and temporal variability of the competition pressure may initiate density-determined fluctuations of the abundance in guppy populations. Preferential reproductive strategies among guppy females may be determined by a compromise between two conflicting requirements: (1) endeavour for a maximum instantaneous rate of increase per female (r-selection) and (2) development of comparatively larger offspring with superior competitive abilities (K-selection) (Pianka, 1970; Stearns, 1976, 1977). The present results indicate that females exposed to low densities with depressed competition pressure exhibited a strategy for maximized fecundity and fertility, whereas intensified density effects caused by high population levels induced reproductive tactics adjusted for production of larger progenies. Production and maintenance of such adaptations are among guppies results of differential selection influenced by pertinent density effects. Depression of individual reproductive output caused by an increased population density under conditions of food restriction (I,V) may be interpreted according to (1) the ecological and physiological stress model and (2) evolutionary theory. The stress model implies an increased release of ACTH and corticosteroids (Lagler et al., 1962) at high densities. Inhibition of vitellogenesis, atresia of ovarian follicles and decreased reproductive success are some of the effects (Ball, 1960), which may be applied to the present studies. High population densities may have induced intensified social pressure (stress) by higher reciprocal interference and subsequent inhibition of reproductive processes leading to reduced fecundity. This feature was evident when a food restriction existed (I,V). Food excess (IV) permitting increased social facilitation of the feeding behaviour (Crawford, 1939; Uematsu, 1971 a, b) may have counteracted negative influences, of high population densities, on ovarian dimensions, gonad weight and reproductive output in the guppy females. Mechanisms implying compensation for detrimental effects of pronounced crowding by intensified ingestion per unit of time and improvement of oogenesis and fecundity may be of great importance in this context. The present results emphasize that relationships between population density and individual reproductive success must be carefully considered for optimal production in fish culture. The second explanation for the occurrence and maintenance of a depressed reproductive

output at increased densities is that guppy females possessing synchronized and inverse feed-back mechanisms in association with fecundity and population density may be selected for. High capacity to respond adequately to current densities could be important prerequisites for optimum reproductive success. Decreased individual fecundity and fertility, still on an optimal level, would form an efficient egocentric strategy when increased density effects indicate keen competition, starvation and high mortality in the future. Production of larger progenies (I) exhibiting increased competitive abilities may compensate for decreased number of embryos per guppy female. Females neglecting this strategy would suffer a comparatively higher mortality among their less competitive offspring. Density-dependent reproductive mechanisms have a great influence on fitness in this context.

IV.2. Nutritional studies (II,III,VI,VII):

The results demonstrate a significantly improved individual fecundity, ovum diameter and size of vitellogenic oocytes in females fed on a comparatively higher protein level. There was also found an increased number of ova, diameter of vitellogenic oocytes, ovarian size and gonad weight among females ingesting ameliorated non-protein amounts. Protein, carbohydrates and lipids represent important environmental factors with a central key function influencing reproductive output in guppy females. Data indicate that the levels of dietary protein and non-protein material have to exceed a certain threshold value in order to cause significant effects on fecundity. Pronounced increments of protein contents in food of either 3.6, 6.5, 8.6 or 15.1 times per female induced a significantly improved individual number of ova, whereas 1.5 times more protein gave no significant influence on egg production. An increase of the non-protein amount per female of 3.6 times resulted in a reinforced fecundity, but 2.8, 2.6, 2.5, 2.3, 2.0 and 1.6 times more non-protein had only insignificant effects on the individual number of ova. Dietary contents of protein and non-protein below some of these levels resulted in a depressed reproductive success. Thus, a minimum protein level and diminutive amount of carbohydrates and lipids may exist for maintenance of a relatively high fecundity. Intensified degeneration and resorption of ovarian follicles (Rosenenthal, 1952, 1955) in addition to genesis of corpora atretica (Lambert & van Oordt, 1965, 1973; Stolk, 1951) under conditions of decreased protein supplies may also have influenced the results. A negative association between follicular atresia and food amount ingested has been observed (Bekker, 1958; Scott, 1962) and increased rates of follicular regression and inhibition of vitellogenesis may also have occurred in the present studies of protein restriction. Protein, carbohydrates and lipids may all fulfil important key functions significantly influencing oogenesis, fecundity, gestation and population dynamics when administered in sufficient amounts to iteroparous fish species with viviparity such as the guppy. Increased total body size, standard length and total weight gain were induced by ameliorated protein supplies. Growth maxima were observed when the dietary protein content was increased 15.1 times per female. An accelerated growth rate could mean an earlier sexual maturity and ingress of intrafollicular gestations. The present findings point

to a noticeably improved nutrient and energy allocation to both somatic tissues, ovarian structures, gametes and vitellogenic oocytes when the amount of essential and accidental amino acids were increased. Current data obviously indicate that elaborated levels of protein, carbohydrates and lipids are indispensable prerequisites for success in hatcheries.

IV.3. Population studies and nutritional experiments (I - VII):

Significant relationships between total body length and number of ova per female were demonstrated (I, III, IV - VI) and reveal an improved fecundity in larger guppy females. Correlations between these variables were also found in other fish species (references given in V). Storage of fertile spermatozoa in ovarian tissues of guppy females (Purser, 1937; Whitney & Hahnel, 1964; Winge, 1937) may have occurred in some of the present studies. Sperm storage could have resulted in delay of fertilization and intra-follicular gestation in order to avoid detrimental effects on embryogenesis under conditions of depleted nutrient supplies. Females without intrafollicular embryos, zygotes, ova and vitellogenic oocytes, but with pre-vitellogenic oocytes were observed (I - VII). Main reasons for this could be (1) degeneration and resorption of secondary oocytes resulting in formation of corpora atretica (Lambert & van Oordt, 1965, 1973; Stolk, 1951), (2) resorption of ova (Rosenthal, 1952, 1955), (3) cyclic development of reproductive units and suppression of vitellogenesis. Variation in number of embryos and ova between females was observed in each population density and in every group of nutritional studies (I - VII). The main reasons are (1) differential feeding rates and reproductive outputs (Gorlick, 1976) in social dominance hierarchies (Nagoshi, 1967) and also (2) genotypic differences of the reproductive capacity. Females possessing intrafollicular ova of different size classes existing in the ovary at the same time were also found (I - VII). This could be the result of (1) an extended reproductive period (Bulkley, 1970) followed by (2) a new vitellogenesis, (3) cyclic development of eggs in addition to (4) degeneration of some ova (Rosenthal, 1952, 1955). Females with intrafollicular embryos and ova simultaneously existing in the gonad frequently occurred in the present investigations (I - VII). This reproductive feature, superfoetation (Scrimshaw, 1944; Turner, 1937, 1940), indicated development and fertilization of ova prior to parturition of embryos progressing in the ovary at the same time. Superfoetation may represent a prevalent reproductive mechanism in guppy females.

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